The one that got away from Smith Woodward: cranial anatomy of Micrornatus (Acanthomorpha: Scombridae) revealed using computed microtomography

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Abstract: The monotypic scombrid fish Micrornatus is represented by a single skull from the early Eocene (Ypresian) London Clay Formation of southeastern England. Although Arthur Smith Woodward substantially increased the diversity of scombrids and scombrid-like taxa known from this deposit, he seems not to have studied the fossil that would later be recognized as Micrornatus. Here we re-examine this specimen using computed microtomography, with two principal aims: first, a revised anatomical account with an emphasis on concealed features; and, second, ‘proof-of-concept’ for the tomographic study of fish crania from the London Clay. Scans reveal new details of the braincase, suspensorium and ventral hyoid arch. We compare the cranial anatomy of Micrornatus with other members of Eocoelopomini, a group also containing the genera Eocoelopoma, Palaeothunnus and possibly Landanichthys. Clarification of the taxonomy and phylogeny of early fossil scombrids is needed, and we suggest that computed tomography will be a useful tool for revealing the anatomical evidence needed to accomplish this goal.

Supplementary material: Micrornatus hopwoodi NHMUK PV OR 36136 PLY files are available at: http://doi.org/10.6084/m9.figshare.1561381

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In his Catalogue of Fossil Fishes in the British Museum (Natural History), Arthur Smith Woodward described numerous specimens from the early Eocene (Ypresian) London Clay Formation (see Friedman et al. 2015). Among these materials was a diversity of forms currently aligned with scombrids (Monsch 2005), a group that has undergone considerable taxonomic restructuring over the past century (e.g. Regan 1909; Gosline 1968; Collette et al. 1984, 2001; Johnson 1986; Carpenter et al. 1995; Orrell et al. 2006; Yagishita et al. 2009; Betancur-R et al. 2013; Miya et al. 2013; Near et al. 2013) but includes a core membership of three percomorph families: Scombridae (tunas and mackerels), Gempylidae (snake mackerels) and Trichiuridae (cutlassfishes).

Smith Woodward’s classification included a Scombriformes containing a variety of lineages now recognized as constituting a polyphyletic assemblage. Apart from a Scombridae equivalent in composition to the ‘core’ Scombroidei of current usage (Scombridae + Gempylidae + Trichiuridae), Smith Woodward’s Scombriformes included carangids, menids, stromateoids and xiphioids, as well as taxa now recognized as pleuronectiforms (Friedman 2008), polymixiids (Patterson 1964) and lampridiforms (Davesne et al. 2014). Smith Woodward’s Catalogue represented a substantial increase in the diversity of mackerel-like taxa known from the London Clay, adding four new genera to Agassiz’s Sphyraenodus: Eothynnus (now interpreted as a carangid; Bannikov 1979), Scombrinus, Eocoelopoma and Scombranphodon. These accounts drew on numerous specimens of each of these new taxa (Eothynnus, 13 specimens; Scombrinus, 35 specimens; Eocoelopoma, 33 specimens).

Given Smith Woodward’s care in reviewing these and other materials from the London Clay, it is surprising that he made no mention of specimen NHMUK PV OR 36136, a well-preserved and uncrushed skull from the Isle of Sheppey, acquired by the British Museum (Natural History) in 1851, several decades before he began work on the Catalogue. This fossil was first described by Casier (1966) in his monumental overview of the London Clay fish fauna, where he placed it as a new species in Smith Woodward’s Eocoelopoma: Eocoelopoma hopwoodi. On the basis of differences related to cranial ornament, dental morphology and patterns of skull roofing bones, Monsch (2005) recognized this individual as distinct from other species of Eocoelopoma, and erected the
analyses. Data that might feed into future phylogenetic reconstructions of teleosts both fossil and modern is desperately needed, but well beyond the scope of this contribution. Instead, we aim to demonstrate the utility of approaches that allow the reconstruction of internal structures. This reflects our second goal: to provide proof-of-concept of this approach for studying fishes from the London Clay (as done successfully in birds from this deposit; Milner & Walsh 2009; Walsh & Milner 2011), as well as three-dimensionally preserved fossil teleosts more generally (Friedman et al. 2015).

New insights on the anatomy of extinct scombrids are particularly topical, given an emerging picture from molecular data placing tunas and their immediate relatives in a previously unrecognized clade characterized by pelagic ecologies (Betancur-R et al. 2013; Miya et al. 2013; Near et al. 2013). Evolutionary timescales for diversification in this group, variously called Pelagia or Scombriformes, vary by tens of millions of years (Betancur-R et al. 2013; Miya et al. 2013; Near et al. 2013; Santini et al. 2013). Part of this ambiguity stems from difficulties in applying fossil-based calibrations in molecular clock studies of scombrids and their immediate relatives, as no extinct member of these groups has ever been placed in a formal, published cladistic analysis (informal or adapted trees are found in Monshch & Bannikov 2012; a formal, but unpublished, cladistic analysis is presented by Monshch 2005)). A re-evaluation of the relationships of scombrids and their immediate relatives in a previously unrecognized clade characterized by pelagic ecologies (Betancur-R et al. 2013; Miya et al. 2013; Near et al. 2013) is given in Casier (1966, pp. 284–286), with minor amendments given in Monshch (2005, p. 476), these are based exclusively on external structure and many aspects of internal morphology remain unclear. Specifically, we have applied computed microtomography (μCT) in order to visualize concealed structure in this unique specimen. This reflects our second goal: to provide proof-of-concept of this approach for studying fishes from the London Clay (as done successfully in birds from this deposit; Milner & Walsh 2009; Walsh & Milner 2011), as well as three-dimensionally preserved fossil teleosts more generally (Friedman et al. 2015).

Materials and methods

Materials examined

All fossil specimens listed below and examined in the course of this study are from the London Clay Formation (Ypresian) of SE England. Provenance data are poor for many of these specimens, but all probably derive from the Isle of Sheppey. For a review of geological context, see Friedman et al. (2015).

- Eocoelopoma colei (Woodward, 1901). NHMUK PV P 26702 (specimen referred to species by Monsch 2005), three-dimensionally preserved neurocranium and sclerotic ossicle.
- Eocoelopoma curvatum (Owen, 1854). NHMUK PV OR 44877 (neotype specimen), three-dimensionally preserved neurocranium; NHMUK PV OR 24613, (specimen referred to species by Monsch 2005), three-dimensionally preserved neurocranium; NHMUK PV P 9455 (specimen referred to species by Monsch 2005), three-dimensionally preserved skull.
- Eocoelopoma gigas (Casier, 1966). NHMUK PV OR 39221, three-dimensionally preserved skull.
- Micrornatus hopwoodi (Casier, 1966). NHMUK PV OR 36136 (holotype and only specimen), three-dimensionally preserved skull (Figs 1 & 2).

Specimen preparation: computed tomography

Historical preparation of the type and only specimen of Micrornatus (NHMUK PV OR 36136) revealed bones on the surface of the specimen, including the external faces of the neurocranium, jaws, preoperculum and part of the suspensorium. We applied μCT in order to visualize anatomical components that remain buried in the clay matrix, without risking damage to this unique specimen through additional mechanical preparation.

Sample scanning. The specimen was scanned with a Metris X-Tek HMX ST μCT scanner in the Imaging and Analysis Centre of the Natural History Museum, London. It was scanned using a 2.5 μm copper filter, with the following settings: 205 kV, 198 μA and 3128 projections.

Segmentation of tomographic data. We segmented the reconstructed series of tomographs using the software package Mimics Research Version 17.0 x64 (http://biomedical.materialise.com/mimics). Segmentation within Mimics can be achieved in a number of ways depending on bone and matrix contrast and other aspects of preservation. These factors greatly influence the quality of the model produced. Pyritization in particular can affect whether the margins and sutures of bones are clearly visible, as the mineral is often apparent as a sheath surrounding individual ossifications or sets of adjacent bones in material from the London Clay (Beckett & Friedman pers. obs. of additional scans). This can make it difficult to use a general thresholding technique. In NHMUK PV OR 36136, there is considerable internal pyrite growth, particularly in the anterior...
portion of the skull. Initially the model (Fig. 3) was built up from a global threshold that selected the majority of the bone. This was then split into individual masks for each ossification, using a combination of the region-growing tool (which populates a new mask with interconnected voxels of the specified grey values) and the 3D edit tool (where sections of bone can be deleted or separated).

These separate masks for each bone were then edited manually, by segmenting the parts of these bones that could not be added to the mask using general thresholding techniques. This approach is particularly useful in cases where there is a very low contrast between the bone and the matrix (e.g. in the middle or on the edge of the specimen), or where there is a high degree of pyritization. The manual technique involves selecting an area of bone visible in cross-section in every nth slice and interpolating between these slices. Where possible this is done using a threshold value, so that only voxels within the area highlighted that fall within a specific range of user-specified grey values are selected. However, in some sections of the fossil bones are so poorly mineralized, or so heavily pyritized, that

Fig. 1. Photos of the fossil NHMUK PV OR 36136 Micrornatus hopwoodi in (a) left lateral view and (b) right lateral view.
they must be added manually without specifying grey values. There are particularly high levels of pyritization in the anterior portion of the skull, around the anterior of the parasphenoid, vomer and hyoid arch.

*Rendering of 3D models.* High-resolution models produced in Mimics were exported as surface (.ply) files. These surface files were then imported into Blender (blender.org) and rendered into two-dimensional high-resolution images.

**Systematic palaeontology**

**Teleostei** Müller, 1845  
**Percomorpha** Rosen, 1973 *sensu* Johnson & Patterson, 1993  
**Pelagia** Miya & Friedman, 2013 in Miya *et al.*, 2013  
**Scombroidei** Regan, 1909 *sensu* Miya *et al.*, 2013  
**Scombridae** Rafinesque-Schmaltz, 1815

**Eocoelopomini** Monsch & Bannikov, 2012  
**Micromus** Monsch, 2005  
**Micromus hopwoodi** (Casier, 1966)  
1966 *Eocoelopoma hopwoodi* Casier, p. 284, text fig. 65, pl. 44, fig. 3.  
2005 *Micromus hopwoodi* (Casier) Monsch, p. 476, fig. 31.

**Description**

**Neurocranium and associated bones**

Casier (1966, fig. 65) provided a drawing of the dorsal surface of the neurocranium indicating the position of sutures. With the exception of the division between the frontals, we had great difficulty in tracing sutures on exposed surfaces of this specimen. Pyritization, combined with the resolution of our
tomographs, does not permit the identification of sutures between most ossifications of the neurocranium. Our references to individual bones below are based on positional comparisons with other scombrids (Starks 1910; Collette & Chao 1975; Collette & Russo 1985) rather than explicit delimitation of ossifications based on visible sutures.

In dorsal view the neurocranium is broad and relatively square, and narrows slightly anteriorly (Figs 4a & 5a). The paired frontals are broad and meet in a suture that is approximately straight, with some minor deviations from the midline. A shallow concavity on the lateral margin of the frontal anterior to the orbit marks the articulation with the elongate nasal (Fig. 3). Fine ornament radiates anterolaterally from the middle of the frontal, immediately above the orbit (Fig. 2a). The frontals surround an opening along the dorsal midline near the rear of the orbit. This opening is subtriangular and narrows posteriorly, and has been interpreted previously as a pineal foramen (Monsch 2005). However, remnants of thin bony laminae are apparent within it, both through visual inspection and in tomographs. We cannot exclude the possibility that the pineal region was completely covered with a thin surface of bone. The median ethmoid sits anterior to the frontals and articulates ventrally with the dorsal margin of the vomer (Figs 4b & 5b). The median ethmoid has a concave anterior margin, conferring a saddle shape in dorsal view that is apparent both externally and from models derived from μCT (Figs 2a, 4a & 5a).

In dorsal view, the posterior half of the braincase bears a series of shallow fossae bounded by ridges (Figs 4a & 5a). Thickenings extending along the posterior and lateral margins of the skull define the outer margins of the more lateral fossa; the pterotic and frontals contribute to the equivalent of the lateral ridge in modern scombrids. These ridges join at the pointed posterolateral corner of the braincase. The lateral and posterior ridges are joined by a pair of low crests that extend anteroposteriorly, subparallel to the midline. Based on comparison with other scombrids, we conclude that the parietals and epiotics contribute to these more medially placed ridges, although we cannot clearly identify the sutures delimiting these bones. Bone appears to be absent from the centre of the lateral fossa defined by these ridges, consistent with the cartilage-filled fontanelle between ossifications that contribute to the equivalent cranial depression in some modern scombrids (e.g. Allis 1903, pl. 4,

Fig. 3. Three-dimensional rendering of the skull of NHMUK PV OR 36136 Micrornatus hopwoodi.
The midline of the skull posterior to the frontals bears a supraoccipital crest, although this is clearly broken dorsally and posteriorly. In combination with the parietal–epiotic crest and the raised posterior region of the frontals, the supraoccipital defines an additional fossa on the dorsal surface of the skull roof. This is shallower than its more lateral counterpart.

In posterior view, the neurocranium is substantially wider than deep. The foramen magnum is triangular in shape. It is continuous with a keyhole-shaped gap that extends dorsally along the midline, terminating at the posterior margin of the supraoccipital and separating bones of the right and left half of the skull. Similar gaps between the exoccipitals are apparent in some modern scoliods (Collette & Chao 1975, fig. 26). The tripartite occipital condyle comprises a pair of dorsal facets borne by the exoccipitals and a large circular facet on the posterior surface of the basioccipital (Fig. 6). The exoccipital facets are kidney shaped, and only narrowly separated along the midline.

Fig. 4. Three-dimensional renderings of the neurocranium of NHMUK PV OR 36136 Microrhadinus hopwoodi in (a) dorsal view, (b) right lateral view and (c) ventral view.
Foramina for the vagus nerve (X) are visible in ventral view lateral to these facets, and are assumed to lie within the bodies of the exoccipitals. The facet on the basioccipital is gently concave. In ventral view, the basioccipital bears a deep sulcus along its ventral midline that opens into the posterior myodome (Figs 4c & 5c). The intercalar is assumed to form the posteroventral margin of the neurocranium. Some sutures can be delimited in this region based on external observation (rather than tomographs), but the complete outline of the bone remains obscure.

Divisions between bones making up the ventral and lateral walls of the neurocranium are unclear. A strong lateral projection from the side of neurocranium, posteroventral to the orbit, represents the sphenotic, and thin sheets of bone applied to the ventral surface of the frontals and defining the dorsomesial roof of the orbital chamber represent the pterosphenoids. However the limits of these
and other bones that contribute to the ventrolateral walls of the braincase (e.g. prootic) are unclear. However, several features are visible on the ventrolateral wall of the neurocranium posterior to the orbit. Most obvious is the strut-like lateral commissure, which defines the outer wall of the trigemino-facial chamber (Figs 4b, c, 5b, c & 6). The foramen for the internal carotid artery lies ventral to the lateral commissure, along the dorsolateral margin of the parapophyseal foramen (Figs 4c, 5c & 6c, d). An unossified area is apparent on both sides of the braincase, immediately posterior to the foramen for the internal carotid. A similar cartilaginous region is apparent in the same position of Scomber, where it is visible in an interior view of the cranial endocavty and marks the division between the prootic and basioccipital (Allis 1903, pl. 4, fig. 8). We suggest that this unossified area also delimits the extent of these ossifications in Micrornatus. The hyoid facet is developed as a shallow, ventrally directed depression (Figs 4 & 5). Additional features are visible on the anterior surface of the postorbital wall (Fig. 6c, d). There is a large midline fenestration for the optic nerve
This opening is separated from the more ventrally located aperture of the posterior myodome by the basisphenoid (Figs 4c, 5c & 6c, d), which bears a slender ventral limb that contacts the dorsal surface of the parasphenoid. A small foramen immediately lateral to the transverse bar separating the opening for the optic nerve and the aperture for the myodome is interpreted as accommodating the oculomotor nerve (III) (cf. Allis 1903, pl. 4, fig. 9). Other apparent perforations in the postorbital wall cannot be identified with confidence.

In ventral view, the most conspicuous feature is the parasphenoid (Figs 4c & 5c). It is splint-shaped in ventral view, and only expands modestly in width approaching its anterior and posterior limits. The parasphenoid bears a short, triangular ascending process at the level of the lateral commissure (Figs 4b & 5b). The posterior margin of the parasphenoid is notched, with short flanges extending along the lateral margins of the rear opening of the posterior myodome. Anteriorly, pyrite growth obscures the suture between the parasphenoid and vomer, as well as the morphology of the vomer more generally. The lateral ethmoids (Figs 4b & 5b) extend from the level of the parasphenoid to the ventral surface of the frontals, and define the anterior margin of the orbital region. They are topologically complex bones: concave posteriorly with two lateral protrusions and an anterior protrusion, resulting in an hourglass shape.

Infraorbital bones and sclerotic ossicles

Sclerotic ossicles are preserved on both sides of the skull (Fig. 3). They comprise anterior and posterior ossifications. The lacrimal (Fig. 7a, b) is a thin, plate-like ossification preserved on both sides of the skull. It extends from the lateral ethmoid to near the posterior margin of the maxilla, and overlaps the dorsal margin of that bone.

Jaws

The maxilla is a long, narrow bone that extends the length of the ethmoid and otic regions of the neurocranium (Figs 1, 3, & 7). In dorsal view, the anterior portion of the maxilla widens laterally to form an articular head. In anterior view, this bears a wide notch marking the point of articulation with the premaxilla. Posterior to the articular head, the body of the maxilla is roughly circular in cross-section. At its posterior tip, the maxilla becomes mediolaterally flattened such that it is plate-like. It is unclear whether a supramaxilla is present. There is a bone on the left side of the specimen that could be interpreted as a supramaxilla (Fig. 7a, b),

Fig. 7. Lateral views of the jaws of NHMUK PV OR 36136 Micrornatus hopwoodi: (a) three-dimensional rendering of jaws and lacrimal in left lateral view; (b) interpretive drawing of jaws and lacrimal in left lateral view; (c) three-dimensional rendering of jaw in right lateral view; and (d) interpretive drawing of jaws in right lateral view. ang, angular; den, dentary; lac, lacrimal; mx, maxilla; pmx, premaxilla.
but comparisons with the right-hand side of the skull suggest that it represents the broken posterior limb of the lacrimal. On the right-hand side of the specimen the region expected to bear the supraramaxilla has been deeply excavated by historical preparation, possibly destroying this bone were it present.

The premaxilla extends most of the length of the maxilla, is robust anteriorly and tapers to a point posteriorly (Fig. 7c, d). The anterior portion of the premaxilla forms a beak-like tip. The ascending process is broken, but appears to have been short. It is accommodated by the concave anterodorsal surface of the median ethmoid. The premaxilla bears a single row of widely spaced, slender teeth. These decrease in length towards the posterior end of the jaw. The right premaxilla bears nine teeth, while the left bone has seven. The maxilla and premaxilla lie parallel to one another.

The lower jaw extends approximately two-thirds the length of the neurocranium. The dentary forms all of the oral border and the anterior two-thirds of the ventral border of the lower jaw. Neither the left nor right dentary is complete anteriorly. The oral border bears nine teeth on the right-hand side and six on the left; these teeth are relatively similar in size and evenly spaced along the oral margin of the bone. The angular forms the posterior portion of the lower jaw, and articulates with the dentary in an elongated ‘v’-shaped contact. A small hook-like extension at the posteroventral corner of the jaw marks the position of the articulation with the quadratojugal.

Suspensorium

Much of the suspensorium is intact. The palatine, metapterygoid, quadrate and hyomandibular are well preserved; the endopterygoid and ectopterygoid are present but heavily pyritized (Fig. 8). The palatine is short, and extends the length of the ethmoid region of the neurocranium (Figs 3 & 8). The body of the palatine consists of a thick rod that bears a thin trapezoidal plate ventrally. The flattened maxillary process of the palatine is long and extends anterolaterally to embrace the anterior head of the maxilla. The palatine is enveloped in sheets of pyrite, making it difficult to determine whether it bore small teeth. Large teeth or tooth sockets, however, are absent. On the left-hand side of the specimen, a suture between the palatine and the ectopterygoid is not distinguishable, but on the right-hand side these two elements have separated taphonomically and are offset from one another. The long, thin ectopterygoid articulates with the posterodorsal margin of the palatine. The posterior half of the ectopterygoid curves ventrally and extends along the anterior margin of the quadratojugal, giving it a gutter-like cross-section.

The endopterygoid is a broad, flat plate. It sits medial to the ectopterygoid, with a concave lateral face. The posterolateral margin of the left endopterygoid curves ventrally to form a plate-like extension. The metapterygoid is fan-shaped, widest ventrally with a large posterodorsal extension marking its articulation with the hyomandibular.

The quadrate is fan-shaped and bears a short posterodorsal process (Figs 1, 3 & 8). The anteroventral condyle articulates with the glenoid of the lower jaw. The symplectic is housed in an elongated notch parallel to the posterior margin of the quadratojugal. The symplectic is preserved in situ on the right-hand side of the specimen. It is a small, narrow bone approximately half the height of the quadratojugal, with a small posterior projection.

The dorsal end of the hyomandibular is expanded as a small head, bearing two facets for articulation with the neurocranium. The anterior facet is circular in cross-section, while the top of the hyomandibular head is broadened to form the posterior articular facet of the head. On the posterior margin of the hyomandibular head is a broad flat surface that articulates with the anterior facet of the operculum. The ventral shaft of the hyomandibular is long and slender, and articulates with the posterior margin of the metapterygoid. An anteriorly directed lamina of bone extends from the head of the hyomandibular to a point dorsal to the midpoint of the shaft. This extension is overlapped by the posterodorsal process of the metapterygoid.

Ventral hyoid arch

The ceratohyals are preserved on both sides of the specimen (Fig. 3), but the anterior ceratohyal on the left hand side is broken in half and displaced from life position. The anterior ceratohyal is narrow in dorsal view and hourglass-shaped in lateral view, with a pronounced constriction in the middle of the bone (Fig. 9). The anterior ceratohyal has a complex anterior articular facet, with a long process that extends under the ventral hypohyal. Only visible on the right-hand side of the specimen, the ventral hypohyal articulates anterodorsally with the dorsal hypohyal. Both the dorsal and ventral hypohyals are elongated cylinders; the ventral hypohyal expands ventrally to articulate with anterior extension of the anterior ceratohyal. A shallow groove extends along the dorsal half of the lateral surface of both the anterior and posterior ceratohyal. On the anterior ceratohyal this is developed as a slit-like ceratohyal window. The posterior ceratohyal is approximately the same height as the
anterior ceratohyal anteriorly, but narrows posteriorly to give the bone a triangular shape. Branchiostegal rays are present, but incomplete. They are narrow and circular in cross-section, but their pattern of articulation with the hyoid bar is unclear.

Opercular series

The opercular series is not preserved in its entirety (Fig. 3). The preoperculum is present on both sides of the specimen, and the operculum is preserved on the left-hand side. The preoperculum is an upright semi-ellipse, with a small ventral protrusion where the preoperculum articulates with the hyomandibular. The preoperculum is approximately the same height as the hyomandibular. The operculum is fragmentary, preserving only the articular facet for the hyomandibular and a plate-like extension dorsally.

Discussion

The challenges of interpreting fossil scombroids

The modern era of scombroid systematics began when Regan (1909) removed a series of families (Coryphaenidae, Rachycentridae, Carangidae, Bramidae, Menidae) present in older classifications.
(including Woodward 1901), and restricted the group to four ‘divisions’: his Trichiuriformes (Trichiuridae and Gempylidae), Scombriformes (Scombridae), Luvariformes (Luvaridae) and Xiphiiformes (Xiphiidae, Istiophoridae, and a series of extinct families). With the exception of the removal of Luvarus to Acanthuroidei (Tyler et al. 1989), a Scombroidei containing these lineages has been a feature of most morphological classifications ever since. Existing cladistic analyses based on anatomy all conform to the hypothesized monophyly of these lineages (Collette et al. 1984; Johnson 1986; Carpenter et al. 1995; Monsch 2000), but this agreement is not universal; some non-cladistic treatments argued that billfishes evolved independently of other scombroids, and that their shared characteristics represented common adaptations to high-speed swimming (Gosline 1968; Potthoff et al. 1980; Nakamura 1983; the latter also rejected billfish monophyly). Molecular evidence strongly supports a polyphyletic origin of the ‘classical’ Scombroidei, which is divided into two independent clades: one including the billfishes, and another containing scombrids, gempylids, and trichiurids, among others (Finnerty & Block 1995; Orrell et al. 2006; Smith & Wheeler 2006; Yagishita et al. 2009; Betancur-R et al. 2013; Miya et al. 2013; Near et al. 2013). Here we accept that Regan’s Scombroidei minus Luvarus is not a natural group, consistent with the overwhelming signal from multiple molecular markers.

Because existing morphological synapomorphy schemes are predicated on the monophyly of the classical Scombroidei, the placement of fossils in association with any of its past members is problematic. Compounding matters, cladistic classifications of scombroids vary substantially from one another, particularly with respect to the intra- and inter-relationships of Scombridae: Johnson (1986) regarded this as a paraphyletic assemblage with respect to billfishes, while Collette et al. (1984) indicate that it is the monophyletic sister group of billfishes. Although a monophyletic Scombridae is resolved in many molecular analyses (e.g. Miya et al. 2013), this is not universal (e.g. Near et al. 2013), and patterns of intrarelationships vary considerably between analyses (compare Miya et al. 2013 and Santini et al. 2013).

Fig. 9. Right lateral view of the ventral hyoid arch of NHMUK PV OR 36136 Micrornatus hopwoodi: (a) three-dimensional rendering of hyoid arch and (b) interpretive drawing of hyoid arch. a.cer, anterior ceratohyal; br, branchiostegal rays; cer.w, ceratohyal window; d.hy, dorsal hypohyal; p.cer, posterior ceratohyal; v.hy, ventral hypohyal.
The placement of Micrornatus

Discord with respect to the relationships of Scombridae is particularly relevant to interpreting the phylogenetic affinities of Micrornatus because it has consistently been identified as a scombrid for the past century (Woodward 1901; Casier 1966; Bannikov 1985; Monsch & Bannikov 2012; but see Monsch 2005). We review the evidence for the phylogenetic placement of Micrornatus here, with the obvious caveats that must accompany such an exercise given the uncertainty surrounding the relationships of scombroids sensu lato.

Many characters that feature prominently in classic cladistic treatments of scombroids (Collette et al. 1984; Johnson 1986; Carpenter et al. 1995) pertain to the gill skeleton or postcranium. Unfortunately, neither is preserved in Micrornatus, although complete gill skeletons are present in other putative scombroids from the London Clay that we have scanned using μCT (Beckett & Friedman, pers. obs.). Micrornatus has non-protrusible jaws (Collette et al. 1984, character 19; Johnson 1986, character 9; Carpenter et al. 1995, character 9), a feature previously interpreted as a synapomorphy of scombroids inclusive of billfishes (and, in the case of Johnson 1986, sphyraenids), but which must now be considered convergent between the two lineages. Micrornatus also lacks an inner row of fang-like premaxillary teeth (Collette et al. 1984, character 18; Johnson 1986, character 32), which has been interpreted as a synapomorphy of scombroids and billfishes. However, the absence of such dentition is certainly a plesiomorphic feature among perciforms (Johnson 1986, p. 5), so derived status in this case depends on the placement of fang-bearing taxa (e.g. trichiurids, gemplyids, Scombrolabrax) as proximate outgroups.

At present, the most compelling evidence for the scombrid affinities of Micrornatus derives from

![Fig. 10. Dorsal view of the neurocranium and median ethmoid (shaded grey) of the holotypes and referred specimens of Micrornatus and Eocoelopoma. All material is from the Eocene (Ypresian) London Clay. Scale bar indicates 10 mm. (a) Micrornatus hopwoodi, NHMUK PV OR 36136 (holotype); (b) Eocoelopoma curvatum, NHMUK PV OR 44877 (neotype); (c) Eocoelopoma gigas, NHMUK PV OR 39221, (holotype); (d) Eocoelopoma colel, NHMUK PV P 26702 (referred specimen; Monsch 2005); and (e) Eocoelopoma curvatum, NHMUK PV P 9455 (referred specimen; Monsch 2005).]
hypothesized links with coeval taxa known from more complete material: *Eocoelopoma* and *Palaeothunnus*. Monsch & Bannikov (2012) recognize these three genera as a clade they call *Eocoelopomini*, united by two cranial features present in all putative members: postero-superior fossae extending to mid-orbit combined with thickenings of the frontals located anterior to these fossae and ornamented with radiating ridges (such features are also common to *Landanichthys* from Angola; Darteville & Casier 1949, fig. 69). Specimens of *Eocoelopoma* from the London Clay are largely cranial, but postcranial material attributed to this genus and *Palaeothunnus* is known from slightly older deposits in Turkmenistan (Bannikov 1985). Both taxa show the presence of two epurals (one in the case of *Palaeothunnus*; Collette et al. 1984, character 7; Johnson 1986, character 36; the latter interpreted this feature as a character of Scombridae inclusive of billfishes, with a reversal in billfishes) and caudal hypurostegy (Collette et al. 1984, character 14; Johnson 1986, character 33; this feature is also shared with billfishes and many other fast-swimming fish groups, and is probably convergent). *Eocoelopoma* has fused of upper and lower hypural plates (Collette et al. 1984, character 34; Johnson 1986, character 39; *Palaeothunnus* retains separate dorsal and ventral plates), which has been interpreted as either a synapomorphy of a subset of Scombridae (Collette et al. 1984) or of some scombrids plus billfishes (Johnson 1986). Additional features of the caudal skeleton of *Eocoelopoma* that support this placement include preural centra 2–4 shortened, and a bony caudal keel (Bannikov 1985; Monsch & Bannikov 2012). On these grounds, Monsch & Bannikov (2012, p. 278) tentatively propose that *Eocoelopomini* is the extinct sister lineage of *Sardini + Thunnini*. More precise statements about the placement of *Micrornatus* await better documentation of anatomy in fossil scombrids and a consistent, more stable hypothesis among modern species that receives support from both morphological and molecular datasets.

### The taxonomy of London Clay scombrids and related taxa

As part of the reassessment of this fossil we revisited the collections of *Eocoelopoma* from the London Clay at the Natural History Museum, London. This deposit yields three species of *Eocoelopoma*: the type species *E. colei* and the attributed species *E. curvatum* and *E. gigas*. In distinguishing *Micrornatus* from *Eocoelopoma*, Monsch (2005) indicated the following differences: the presence of pineal foramen in *Micrornatus* v. absence in *Eocoelopoma*; fine ornament ridges of frontals in *Micrornatus* v. coarse ridges in *Eocoelopoma*; concave anterior margin of the median ethmoid in *Micrornatus* v. convex margin in *Eocoelopoma*; and slender teeth in *Micrornatus* v. stouter ones *Eocoelopoma*. Based on our visual and tomographic re-examination of *Micrornatus*, we are not convinced that the putative pineal foramen in this taxon is a genuine biological feature rather than a taphonomic one (see above). We do, however, agree that the three other features cited by Monsch

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**Fig. 11.** Dorsal views of neurocrania of probable Eocoelopomini from deposits other than the London Clay. (a) *Eocoelopoma portentosa*, Palaeontological Institute of the Russian Academy of Sciences, Moscow, PIN 1762-85 (redrawn from Bannikov 1985), from the earliest Eocene Danatinsk Formation, Turkmenistan. (b) *Palaeothunnus parvidentatus*, PIN 3363-22, from the earliest Eocene Danatinsk Formation, Turkmenistan. (c) *Landanichthys moutai*, from the late Paleocene of Angola (redrawn from Darteville & Casier 1949).
(2005) distinguish *Micrornatus* from the type species of *Eocoelopoma, E. colei*. To these differences we add two others that relate to the geometry of the skull roof. First, the lateral margins of the frontals in *Micrornatus* are convex posteriorly but are straight to slightly concave anteriorly, in contrast with conspicuous convexity along the same margin in *E. colei* (Fig. 10). Second, the dorsal surface of the frontals is convex along the midline in *Micrornatus*, whereas this area is marked by a concave pit in *E. colei*.

These observations might have some bearing on the taxonomy of eocoelopomines from both the London Clay and other deposits. First, we found that the neotype specimen of *E. curvatum* (NHMUK PV OR 44877) shares features with *Micrornatus* not apparent in *E. colei*: fine ornament of the frontals (Fig. 10b); straight or concave anterolateral margins of the frontals; convex dorsal surface of the frontals; slender teeth. We also note that the holotype of *E. gigas* shares with *Micrornatus* and *E. curvatum* a median ethmoid with a concave anterior margin in dorsal view and a convex dorsal surface of the frontals. Referred material of *E. gigas* shows very slender teeth on the premaxilla (Monsch 2005, fig. 28), resembling those of *Micrornatus*.

Type specimens of *Micrornatus* and *E. curvatum* are of comparable size, but are both substantially smaller than material of *E. gigas*. We are uncertain at present if differences between these smaller specimens and *E. gigas* are taxonomically relevant or instead represent ontogenetic variation. In any case, it seems prudent to delay any formal taxonomic evaluations until more data, including that derived from µCT, are available for relevant specimens. However, in light of our preliminary observations, we suggest that subsequent analysis might require reassignment of some London Clay specimens of *Eocoelopoma* to *Micrornatus*.

More broadly, it is possible to extend this contrast between 'Eocoelopoma-like' and 'Micrornatus-like' eocoelopomines to consider examples from other deposits (Fig. 11). Bannikov (1985) described two new species of large scombrid from the earliest Eocene Danatinsk Formation of Turkmenistan: *Eocoelopoma portentosa* and *Palaeeothenus parvidentatus*. In terms of overall geometry of the frontals, *E. portentosa* is more similar to *Micrornatus* than *E. colei*. In contrast, the strongly convex lateral margins of the frontals of *Palaeeothenus* closely resemble those in the type species of *Eocoelopoma*. A further taxon that can be considered here is *Landanichthys*. From the Paleocene of Angola, this genus is potentially the oldest fossil scombrid. Some material described and figured by Darteville & Casier (1949, fig. 69, pl. 21) shows diagnostic features of Eocoelopomini (Monsch & Bannikov 2012). The frontals as reconstructed by these authors are more similar to those of *Micrornatus* than *Eocoelopoma*, and appear to be concave anterior to the pineal region (Darteville & Casier 1949, fig. 69). The teeth in *Landanichthys* also appear to be relatively slender, as in *Micrornatus*. Darteville & Casier (1949, fig. 69) show a median ethmoid with a convex anterior margin as in *Eocoelopoma*, but this is not apparent in their plates. However, we note that the material assigned to *Landanichthys* is morphologically highly variable (see Darteville & Casier 1959, pl. 38), and might in fact belong to multiple genera. As with the taxonomy of London Clay eocoelopomines, we do not advocate any taxonomic changes before the anatomy of these species is better understood and the polarity of the characters in question is better constrained. Instead, we outline these observations here to provide a roadmap for future investigation.

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References


COLLETTE, B. B. & RUSSO, J. L. 1985. Morphology, systematics, and biology of the Spanish mackerels...
(Scomberomorus, Scombridae). 


